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## Notes on the anatomy of *Parosela spinosa* (A. Gray) Heller

AMELIA RICHARDSON GOODLATTE

(WITH PLATE 29)

The synonymy of this plant is considerable and though the generic name *Parosela* of Cavanilles has priority, in the somewhat scanty literature on the species it usually appears as *Dalea*. It belongs in the order Papilionaceae under the tribe Galegeae. The species is distributed from Arizona northward to Colorado and the California desert and southward to Sonora and Lower California. In stature it is a small tree, sometimes attaining a height of 18–20 feet, with a short trunk and very numerous branches. It is densely spinose, the spines being apparently modified branches, and the older stems are covered with a rough scaly light brown bark. The younger portions, up to stems of the third year, are densely clothed with hairs, and both the stems and spines bear small epidermal emergences or scales, and a few leaf-buds. These, together with the numerous large glands which form noticeable brown spots and protuberances on the surfaces of spines, stems, and leaves, give a decidedly rough and lumpy appearance.

The hairs are of a single type; each consists of two short basal cells and a long, pointed end-cell, the outer part of the walls being cutinized, especially in the basal cells, while the remainder is formed of unmodified cellulose. The small scales or epidermal emergences are conical in shape, hollow in the center, their walls formed of two or three layers of small, nearly cubical cells, the outer ones cutinized like the epidermis.

The system of branching proves to be one of the most interesting of the external features. The superficial appearance is almost that of a dichotomous branching, but investigation shows that in every case a branch arises from a leaf axil. The apparent confusion is due to the fact that the spines are really the main axis transformed, while the axillary shoot, continuing to grow, takes the place of the main axis and itself gives off a shoot, which, developing rapidly into another branch, in its turn gives rise to a

spine and a shoot. Thus, with very few exceptions, in the material examined, there was a regular alternation; first, an axillary shoot, becoming the axis, the main axis being arrested and developed into a spine, then a fork with both axis and shoot developing into equal branches, then again, on each of these a spine and a shoot, and so on. At the growing tip it can be seen that the transformation of axis into spine takes place at a very early stage, the tip becoming horny and the stereome tissue strongly developed before the shoot is well out of the enfolding leaf and considerably before the formation of the axillary shoot which is to take its place as axis.

The most striking internal characters are, in general, the great development in the stem of chlorophyl-bearing tissue to assume the functions of the fugacious leaves, the occurrence in great numbers of crystals of calcium oxalate, and especially the very general distribution and prominence of glands and secretory apparatus.

The leaves, as has been said, remain on the plant only a very short time, and are comparatively few, even in the season. The minute paired stipules each have a large, persistent gland at the base, of the same anatomical character as the glands which are scattered irregularly over the stem and leaf. The hairs cover both surfaces of the leaf, clustering most densely in an irregular arrangement around the stomata. Weyland finds it characteristic of the tribe of the Galegeae, almost without exception, that the stomata are surrounded by cells arranged without any special order, neighboring the guard cells. *P. spinosa* possesses this character in common with the rest of the tribe. The stomata occur on both surfaces of the leaf, but are more numerous on the under side. They are simple in type, the guard cells not being even deeply sunk, though their outer walls are heavily cutinized, in common with the other epidermal cells.

In addition to this layer of cutin, the epidermis of the leaf is noteworthy because of the occurrence of rhomboidal crystals of calcium oxalate in a few of its cells. In regard to the shape of the crystals found by him in the epidermis of the single species *Dalea versicolor* Zucc., Weyland describes them as being short and rod-shaped, the cells containing them lying either singly or in groups, and being smaller than the surrounding cells. In *P. spinosa*,

however, the crystals are distinctly rhomboidal and the small cells containing them are always single in the midst of the larger, ordinary cells (FIGURE 3).

Crystals, in greater or less numbers, in the accompanying tissue of the vascular bundles and in the palisade cells, Weyland finds to be a general character for the order, and he further states that those in the palisade cells are rod-shaped throughout the genus *Dalea*, while the rhomboidal form also occurs in some species. This proves to be true in the case of *Parosela spinosa*. In the layer of cells immediately under the epidermis, and in the mesophyll in general, these rhomboidal crystals are very numerous, especially in the cells surrounding the bundle-strands. The crystals in the palisade tissue are rod-shaped and sometimes partly imbedded in the cell-wall.

The further structure of the leaf is quite simple. It consists of palisade and spongy tissue, the leaf-edges being rolled so that the palisade cells extend round to the under side. The bundles are concentric, surrounded by a considerable layer of stereome tissue, and around that again, as has been mentioned before, a layer of cells with numerous crystals. Weyland cites the case of *Dalea polyadenia*, where these cells with crystal-complexes apparently take the place of bast-fibers as strengthening material, and it may very well be that in *P. spinosa* also they are of auxiliary use in giving rigidity to the leaf-bundles.

The secretory apparatus of the leaves can best be discussed in connection with that of the stem, as the anatomical character of the two is the same. The stem up to the third year has a highly developed chlorophyll-bearing tissue in the cortex, consisting of five or six rows of palisade cells. The stomata are of the same simple type as those of the leaves, being perhaps rather more deeply sunk, in a pit formed by the thickened outer walls. The epidermis has a heavy outer layer of cutin from a very early stage, and this increases until in the third year the entire outer wall, and the radial wall as well, are completely cutinized. As in the leaves, rhomboidal crystals are sparsely scattered through the epidermal cells. The hairs form a thick coating until the formation of the periderm supplants the primary cortex.

Sanio, speaking of periderm formation in general, states that

“Der Sitz der Korkbildung ist übrigens für jeden Species, ja man kann sagen Gattung, constant.” Solereder, on the other hand, quoting as authorities Sanio, J. E. Weiss, and Douliot, on cork formation in the Papilionaceae, says that the position of the cork-forming layer differs not only within the limits of a genus but also “bemerkenstwert ist, dass zuweilen bei derselben Art der Ort der Korkentstehung zwischen der zweiten und sechsten Zellschicht der primären Rinde wechseln kann.”\* Weyland finds that in *Dalea*, in the genus as a whole the cork is formed in the second to sixth cell-row of the cortex. In the plant under discussion it is formed, however, on the very inner row of the primary cortex, immediately outside the primary stereome bundles. This would be about the ninth or tenth row, as the number of rows of palisade cells is variable. Hence there is considerable variability in the genus in this respect (FIGURE 4).

A cross-section of a young stem shows, first, the epidermis, with a layer beneath it of cells containing rhomboidal crystals; then five or six rows of palisade cells, many of them containing rod-shaped crystals; then, a layer of parenchyma cells, with rhomboidal crystals; next, the row of collateral bundles and a cambial ring, rather ill-defined, each bundle being accompanied on the side toward the periphery of the stem by a strand of primary stereome tissue. In the center, of course, are the pith cells, with rather thickened walls, some of them transformed into tracheidal parenchyma with simple pores, and many of them, especially those nearest the wood, containing rhomboidal crystals, sometimes in the cell-cavity, sometimes imbedded in the wall. The only interruption in the simple regular character of the stem structure is the occasional appearance of a few cauline bundles, of the collateral type, accompanied by a stereome strand outside the leptome (FIGURE 5).

As the young stem develops, the layer of cutin, as has been remarked, becomes more strongly developed. When the cortex is supplanted by cork cells the outer ones of these have cutinized walls, the inner (phellogen) layer retaining unmodified cellulose walls. Traces of suberin appear in a few cells of the hadrome,

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\* Anat. Dicot. 313.

from the third year on. The crystals are increasingly numerous as the stem develops. Lignification begins, naturally, in the ducts and tracheids even of the very young stem, and proceeds as the plant grows older, through the walls of the primary stereome, the pith, the inner walls of the parenchyma cells lying next the primary bast bundles, the walls of the secondary stereome, of many scattered palisade cells, and finally occurs in the cells of the bark when this is formed in the sixth year. As the lignified areas increase, the areas containing walls of unmodified cellulose become reduced to those of the leptome, cambium, phellogen, and whatever remains of the palisade tissue. Starch is found from the first to the third year in the contents of the palisade, pith, parenchyma, and medullary ray cells. After this it disappears as the stem becomes less and less an assimilating organ. Proteids, likewise, occur in conjunction with the green tissue and decrease with it.

In the parts of the stem which become modified into spines the process of lignification takes place much more quickly than in the stem that continues to grow. In place of parenchyma cells a stereome ring fills the spaces between the hadrome masses of the bundles. This is especially noticeable as a point of difference between a very young spine and a very young shoot (FIGURES 1 and 2). After this rapid development of tissue that serves to give strength and rigidity, the growth of a spine is limited to simple thickening and enlarging, for there is no secondary thickening.

In the growing stem secondary thickening takes place according to the ordinary dicotyledonous type from a cambial ring. The sieve-tubes are comparatively short and wide. The vessels differ greatly as to size, but all have simple, oval pores, as is characteristic of the family. The walls of the smaller tracheids are spirally thickened. The medullary rays, as usual in the greater number of Papilionaceae, consist of about three cell-rows, somewhat increased toward the outer part in a wedge shape.

Solereider\* quotes Saupe to the effect that the medullary ray cells of the Galegeae are small and round in tangential section. In this case, however, they prove to be oblong and almost rectangular. The wood-prosenchyma cells, where they come into contact with the ducts, have, like them, simple oval pores. There

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\* *Loc. cit.* 310.

are no distinct bundles of secondary bast, not in direct contact with the medullary rays and marked off by a distinct sheath. On the contrary, the secondary stereome is in direct contact with the medullary rays and with the wood. The masses are composed mainly of prosenchymatic or perhaps sclerenchymatic cells, while those of the bast type, with long, pointed ends, are mixed with them in small groups.

The secretory system is extremely well developed, all the varieties of internal secreting organs that are mentioned as occurring in the tribe being found in this species. (This does not include the glandular hairs possessed by a few Galegeae.)

The material used for this work was, first, a dried herbarium specimen which was soaked in a mixture of glycerine, alcohol, and water, to make cutting possible, and afterwards some branches that had been obtained in a living state, through the courtesy of Dr. D. T. MacDougal, but were preserved in the same mixture. Probably something in this method of preserving affected the secretions of the glandular tissues. At all events, all tests for determining their exact contents were unsatisfactory, so that the only conclusion to be obtained is that, since they are analogous in anatomical structure to the organs tested by other observers, their contents are presumably of the same nature.

Throughout the stem and spines there are strands of elongated cells with thin walls and a large cavity, sometimes lying singly, but more often two or three together, in the innermost layer of the primary cortex. In some cases they are immediately adjacent to the bundles of primary stereome, in others they lie opposite the medullary rays (FIGURE 5). Trécul found a similar set of cells with tannin contents in the cortex and also on the outer edge of the pith in *Dalea alopecuroides*. He describes them as "ces sortes de vaisseaux à tannin dont les cellules ne sont ordinairement perforées." Baccarini describes similar ducts in many Leguminosae, which he says may appear in one stage of the plant's growth and disappear subsequently, or may be permanent. These tannin elements are situated: 1, around the pith and outside the stereome; 2, in the periphery of the pith, grouped around the vascular apex of the wood triangle of each bundle, and on the sides of the stereome; 3, around the pith, within the stereome and on its sides;

4, around the pith and within the leptome. These tannin elements are not of invariable occurrence, he finds, in the Leguminosae, and part of the tribe of the Galegeae is without them. *Dalea*, however, belongs to the series provided with this sort of secretion organ. These ducts contain in addition to tannin, he says, albuminous material which will stain bright yellow in iodine, although the tannin interferes somewhat with the reaction. Weyland verifies Baccarini's results in general, but finds that what he interpreted as a transitory appearance of tannin-bearing elements is due to the difference of the contents of the ducts at different stages. In the young stem the contents are almost wholly albuminous and the tannin appears later, which explains, he adds, the great size of the ducts relative to the amount of tannin contained.

In *Dalea*, Weyland observed these ducts in the pith, Trécul in the pith and the primary cortex as well. In the species under discussion, as far as the available material showed, they occur only in the cortex. As has been said, the tests to determine the contents were most unsatisfactory. The ducts were filled with a substance of red-brown color, and this of course made all those tests for tannin which depend upon a red or a brown color-reaction, unavailable. Copper acetate, iron sulphate, and iron acetate, which should give green, black, or blue color, had apparently no effect. It seems probable that the preserving liquid must have affected the contents in some way, although the liquid itself, when tested for tannin, showed no result, so that this could not have been extracted in any large quantity. The arguments, then, for considering these ducts as part of the albuminous-tanniferous apparatus similar to that of other members of the genus and tribe, are simply based upon the similarity in structure and position. The similarity in structure is at once apparent and that in position is evident when one considers Baccarini's statement that the cells normally lying on the sides of the bundles of hard "libro," are sometimes pushed out till they lie between the bundles.

Another type of secretory organ which is very prominent in *P. spinosa* is an ovoid schizogenous gland with an opening to the exterior through a small slit, and surrounded by a firm layer of close-set cells, which show traces of lignification, lined by a layer of papillary epithelium, with densely granular cell-contents, light



brown in color (FIGURE 6). Weyland speaks of finding only traces of this epithelium at an early stage in the formation of the gland, and says that it later breaks down and a schizogenous-lysigenous gland results. In the species *P. spinosa* this is not the case, as the epithelium is plainly marked even in a gland occurring on an old spine, where it is presumable that the gland is of a considerable age. It is glands of this type which form the lumps on the young branches, alluded to by Solereder, and which occur at the bases of the stipules. They occur in numbers in the palisade tissue of the primary cortex, but are naturally absent from the older branches on which the periderm has supplanted the cortical tissue.

In the attempt to decide on the nature of the contents secreted by these glands, we have again to record no result. In this case it would seem that the contents have been extracted. Weyland finds round glands of the same type in all the genera of the subtribe Psoraleae that he examined. They contained a light or dark yellow resin, which was soluble in alcohol. The occurrence of these glands with resinous contents is a character for divisions greater than a genus, he claims. Therefore, since glands of the same structure and position contain resin in other species of the genus and subtribe, and since the resin is soluble in alcohol, it seems safe to conclude that the contents were resinous and have been extracted by the alcohol in which the material was placed.

This completes the secretory apparatus of the stem. The leaves contain the same round glands, which appear in either the palisade or spongy tissue, opening toward either surface. No trace of tannin ducts nor of the single isodiametric tannin-secreting cells, nor of the layer of tannin cells in the mesophyl, mentioned by Baccarini as present in the group, could be found. In addition to the resin-bearing glands, however, the leaves contain a peculiar type of gland, the so-called intercellular glands. These are composed of elongated cells which have split apart from each other, so that in the mature gland they present the appearance of strands of tissue running through the cavity of the gland. Around the whole is a sheath of close-set cells, developed from the mesophyl (FIGURE 7). It is only in the mesophyl tissue and opening on the under side of the leaf that glands of this type occur. Their contents are small pieces of hardened brown stuff,

which is undoubtedly tannin but refuses to respond to any of the tests, like the tannin in the other cases. Solereder describes an exactly similar gland in *Psoralea*. It is the brown coloring of these glands which causes the noticeable brown spots on the leaves of dried material in this species.

This completes the survey of the anatomical characters of *Parosela spinosa* as far as they have been ascertained. The work was done under the direction of Dr. Herbert M. Richards, to whom thanks are due for his many kind suggestions and encouragement.

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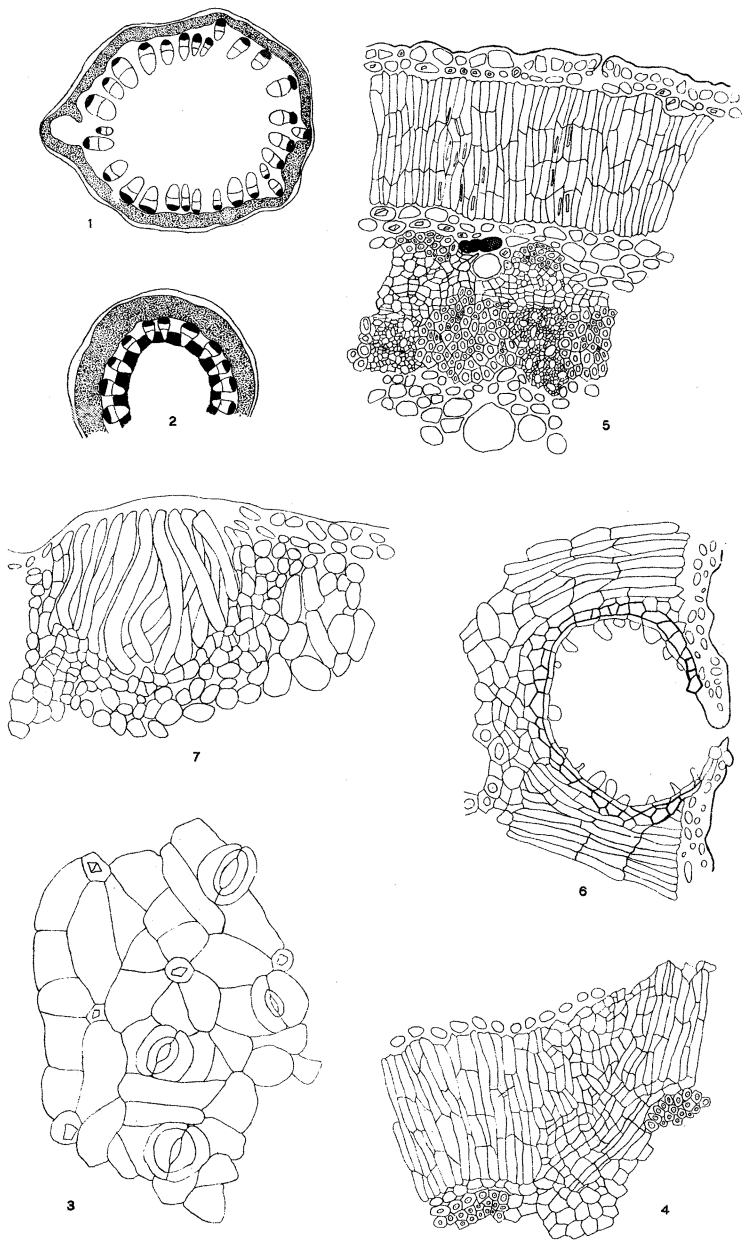
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#### Explanation of plate 29

1. Stem in first year, showing distribution of main tissue areas. Chlorenchyma, stippled; stereome, black; vascular bundles indicated in outline. Magnified 12 diameters.
  2. Spine in first year, as above, showing the greater development of the stereome. Magnified 12 diameters.
  3. Surface view of epidermis of leaf. Magnified 250 diameters.
  4. Periderm formation in stem of third year. Magnified 136 diameters.
  5. Transverse section of portion of stem in third year. The vessels indicated by cross-hatching contain the dark brown albuminous substance. Magnified 136 diameters.
  6. Gland in stem. Magnified 250 diameters.
  7. "Intercellular" gland of leaf. Magnified 250 diameters.
- The figures were all drawn with the aid of an Abbé camera, and the magnifications given above are  $\frac{2}{3}$  of that of the original drawings.



GOODLATTE, THE ANATOMY OF PAROSELA SPINOSA